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Evolution of Australia's Unique Flora and Fauna in Relation to the Plate Tectonics Theory

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Abstract: The Plate Tectonics Theory shows us a different world. Instead of a masses stand high above the heavier masses. The oceans cover the lower heavier rocks, continuous crust, we see a jigsaw of plates with active interfaces. The lighter rock and the high standing lighter rocks are the continents. These two environments of land and sea are ancient, so each has its own ecologic and evolutionary systems; albeit they influence each other strongly.

Threaded through the oceans are some 60,000 km of submarine mountain ranges, often split down the middle with rift valleys. From these rifts new crust oozes out and the ocean floor glides slowly away. Drift rates average 2-3 cm per year. Where the deep trenches line the edges of continents, in areas peppered with seismic centres and volcanoes, the heavy ocean crust is subducted beneath the light continental crust and re-absorbed. The gigantic pressures there, attended by great chemical and physical changes, often push up mountain ranges. Australia experiences mild tectonic activity because it is in the middle of a plate, but New Guinea and New Zealand experience strong seismic, volcanic, and mountain-building activity because they are on the edges of a plate.

The Plate Tectonics Theory envisages all the continents as welded, in the Mesozoic, into a single land mass, Pangaea. Then a big split occurred that divided the mass into Laurasia (Northern Hemisphere land) and Gondwana (Southern Hemisphere land). These in turn broke up into the continents we know. Australia is believed to have broken from Antarctica then drifted away (probably well separated events) between 100×10^6 yr and 50×10^6 yr ago. When the continents parted they shared a common biota, but the longer they were isolated, the more divergent their floras and faunas became. Thus during the Cainozoic there has been a great increase in the diversity of living things. Australia has drifted northward, it is claimed, from cold climates to warm ones, from humid to desertic latitudes. The continent's climate has been complicated by the changes in world climate.

The new theory thus avers that: (a) The crust of the earth is far more mobile, plastic and changing than previously believed. (b) Life on the earth has had to contend with far greater changes than previously envisaged.

The author proposes that the Australian flora and fauna have suffered two major revolutions: (a) After separation from Antarctica, the Mesozoic fern/conifer flora was supplanted by the Australian Tertiary conifer/*Nothofagus* flora, when rainforests were widespread (e.g. Duigan, 1966). (b) The humid Tertiary climate gave way to the modern dry conditions. At this time *Eucalyptus* and *Acacia* came into their own. Massive adjustments by the fauna were necessary. Radiation in both flora and fauna occurred to take advantage of the new environments. In the opinion of the author this radiation is still going on.

INTRODUCTION

Our subject is as wide as the world and as deep as the earth's crust. It is multi-disciplinary. It involves many sciences, including geophysics, geology, geomorphology, geochronology, geochemistry, seismology, botany, zoology and palaeontology. No one can master it all, yet

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the basic ideas are straightforward. The Theory of Plate Tectonics is like the Theory of Relativity in that its complexities cannot be comprehended immediately. Yet its fundamental tenets are simple. These we will briefly outline, and examine their implications for Australia with its unique flora and fauna.

Australia has climates from cold to temperate to tropical, but the first explorers did not find on this island continent samples of all the types of animals and plants familiar to them, and proper to those climates. Instead they discovered many families of plants and animals which the world had never seen before. The early records catch this first reaction to things wholly remarkable, some almost unbelievable. Such a feeling I had in the Mohave Desert north of Harold, California, when I stood in front of a Joshua Tree for the first time. I felt as if I had landed on another planet.

It was difficult enough for the first explorers to have to report that in Australia swans were black whereas everyone knew swans were white. It was at first quite unbelievable when they reported the platypus: it had fur like a mammal, laid eggs like a bird or reptile, had a bill and webbed feet like a duck, yet suckled its young. From New Zealand the bones of a fossil bird (moa) sent to Professor Sir Richard Owen in London at first seemed quite incredible—a bird 4·5 m high! However, he found that the bones were real and the giant *Dinornis* did exist.

Another puzzle in Terra Australis Incognita was that there were rats, mice, cats, dogs, moles, rhinoceros[1], badgers[2], tigers[3], lions[4], and so on, but instead of being placentals as they were known in other countries then, they belonged to the Marsupialia, an Order almost extinct in the rest of the world. Moreover, Australia had its own Devil—the Marsupial Devil[5].

In this strange world of Australia there was another anomaly. Most of the placental groups had their marsupial counterparts, but with one remarkable exception. There were no marsupial horses and cows. Instead, the grasslands and savannahs were occupied by curious animals without parallel elsewhere—the kangaroos and their ilk. The large herbivores elsewhere had four legs, but the kangaroo only two, used for a hopping locomotion. The tail is adapted as a balancing organ.

At the time Australia was discovered, each species was thought to have been created individually, but nevertheless many of the highly specialized beasts were regarded as oddities. The emigrants from Europe found this very difficult to explain. Biologically, the continent is a world all its own, a museum in which all the world is interested. The uniqueness of the Australian flora and fauna has been explained in two ways: (a) the traditional view, involving a static isolated continent related to Asia, and (b) the modern view, involving a drifting continent and relationships with Gondwana countries (Antarctica, South America, Africa and India) (Fig. 1).

EXPLORERS' OBSERVATIONS

Before the views on the origin of Australia's flora and fauna are outlined, it should be noted that Australia's physical characters also require explanation. The first explorers were from humid Europe, but in Australia they discovered the driest continent. However, the broadleafed flora of a humid forest is found fossil in present deserts (e.g. Balme & Churchill 1959). Laterite, the soil of monsoonal rainforests, occurs over thousands of square kilometers of desert country (Fig. 2).

The first explorers came from a continent with a varied terrain of high mountains. They knew and loved their Alps. They had discovered India which has the highest mountains in the world. By contrast, they found Australia a continent without high mountains, and indeed it is the flattest continent. This also requires explanation, and the Theory of Plate Tectonics has one.

CONTINENTAL RAFT

Another physical feature (among many that could be listed) is the shape of the continent. For example, why has Australia a concave southern edge? To get the geologic viewpoint of the continent, strip off in your imagination the mantling ocean, and see the land for what it is (Fig. 1). On this view, Bass Strait, Torres Strait, and such have little meaning. They are shallow furrows in a high-standing continent. With comparatively steep-walled ramparts, the continent stands some 4000 m (over two miles) above the plain of the deep ocean floor. The edge of the continent is not the present coast (an ephemeral boundary), but the rim of the continental shelf. Addition of the shelf makes Australia one third larger, adding another $1 \cdot 3 \times 10^6$ km^2. Using the shelf rim gives the continent a different shape as well as a larger size. In Fig. 1 Australia stands above the ocean floor as a giant raft of lighter continental rocks (sial) in a plate of heavy oceanic rocks (sima), all slowly gliding northwards.

The traditional view could explain Australia's shape only by saying it was made that way. Plate

[1] Nototherium. [2] Wombats were at first called badgers, hence the Badger River in Tasmania. [3] *Thylacinus.* [4] *Thylacoleo.* [5] *Sarcophilus.*

Fig. 1—Australia in relation to the ocean floors. New Guinea, the mainland and Tasmania constitute a single raft of continental rocks. During the low sea-levels of the Quaternary they formed one land mass. (Reproduced by kind permission of The National Geographic Society.)

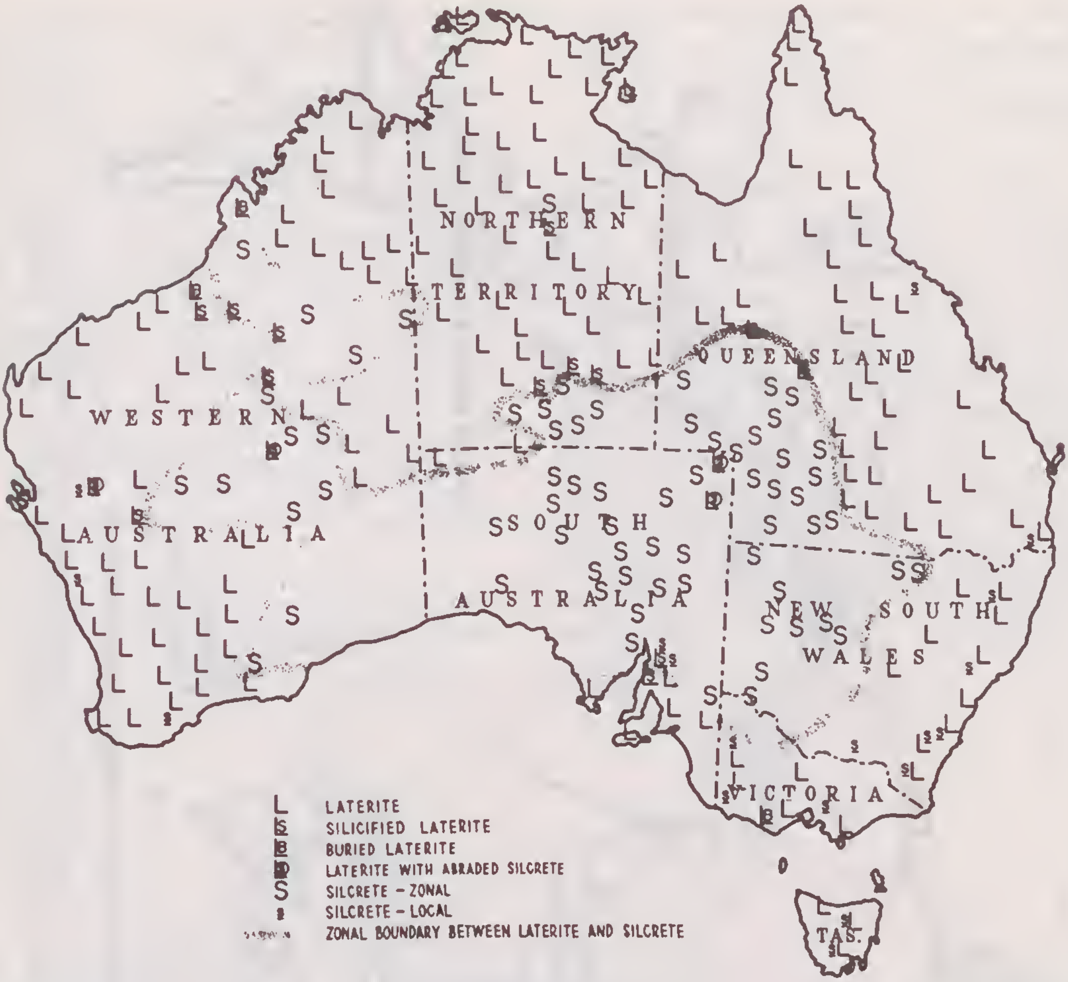

FIG. 2—Distribution of laterite and associated materials throughout Australia (after G. G. Stephens). Laterite is a product of monsoonal rainforest, and is now forming in only a comparatively small area in northern Australia.

Tectonics explains it by its fit with the other land masses to which it was attached. The concave southern edge of the continent fits the convex northern edge of Antarctica.

TRADITIONAL VIEW OF AUSTRALIAN FLORA AND FAUNA

Let us now return to the biologic side of our subject, and review briefly the traditional and modern views of Australia's unique biota.

When Charles Darwin published his 'Origin of Species' in 1859, the view was almost universally held that Australia was where it was and contained what it did because it was created so, and was meant to be so. This static view was inimical to dynamic concepts. People looked back and not forward. Change was not anticipated, but nevertheless the leaven of the Renaissance was working. Already the idea of a flat earth at the centre of the universe had given way to the idea of a spherical earth spinning round a central sun. People came to see that Nature works through inbuilt mechanisms. So they accepted this view of the physical world, but thought the biologic world was different.

A second shock wave was caused by the mild and retiring Charles Darwin. He showed that not only the inanimate world but also the animate world is governed by inbuilt processes. Darwin said that change is constant, and that life is continuously evolving under the guidance of natural selection—another inbuilt mechanism. People in time came to accept this idea, but thought that man must be an exception, because as a self-

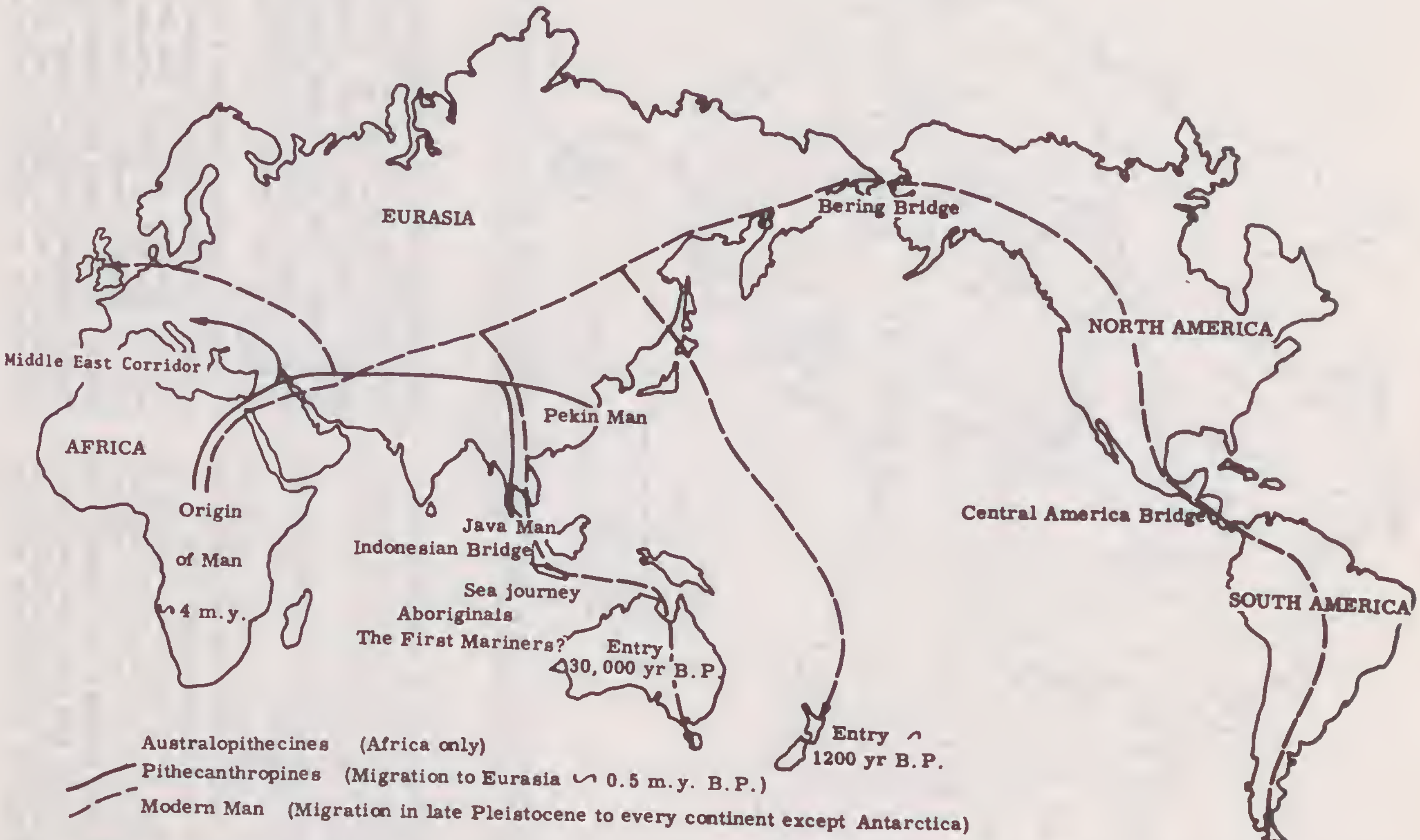

FIG. 3—Map showing dispersion of man. After living for ~ 3·5 m.y. in Africa hominids (*Homo erectus*) spread to Eurasia ~ 0·5 m.y. ago via the Middle East corridor. In the late Pleistocene *Homo sapiens* peopled the whole earth except for Antarctica.

conscious thinking being capable of value judgements, he is so different from the rest of the animal kingdom.

The discoveries of recent years have provided a third shock wave, this time to the thinking about man. The large numbers of fossil hominids discovered prove that evolution applies as much to man as to any other member of the animal kingdom. The findings are summarized in Fig. 3.

Thus after a long (and at times painful) mental odyssey, people have come to accept change and evolution as important principles in astronomy, geology, biology, palaeontology, anthropology, and indeed in every field of learning. The new world view left only one thing stable—the continents—but these also are now considered to be mobile and evolving, according to the Theory of Plate Tectonics. The physical changes envisaged have enormous implications for the history of life in Australia.

Forty years ago the generally accepted opinion concerning the Australian flora and fauna was that they: (a) developed endemically, or (b) were transported to the island continent from Asia by:

i. their own efforts, such as birds flying and crocodiles swimming,
ii. natural rafts, such as rats in drifting logs, and
iii. land bridges now destroyed (Fig. 4).

For Australia, the theory of a land bridge to Asia was never really satisfactory, either geologically or biologically. For example, if marsupials crossed from Asia to Australia (or vice versa), why are there not many fossil marsupial faunas in Asia? But in spite of search none has yet been found. Also if the marsupials crossed, why not the placentals, as both appear to have evolved about the same time? It may be that the desire to find another answer caused some to jump at the idea of 'Continental Drift' in the early stages when the evidence was inadequate. In 1965 the Royal Society (London) held a Symposium on Continental Drift, at which Professor Westoll said, 'Perhaps more dubious and unconvincing "evidence" has been published in

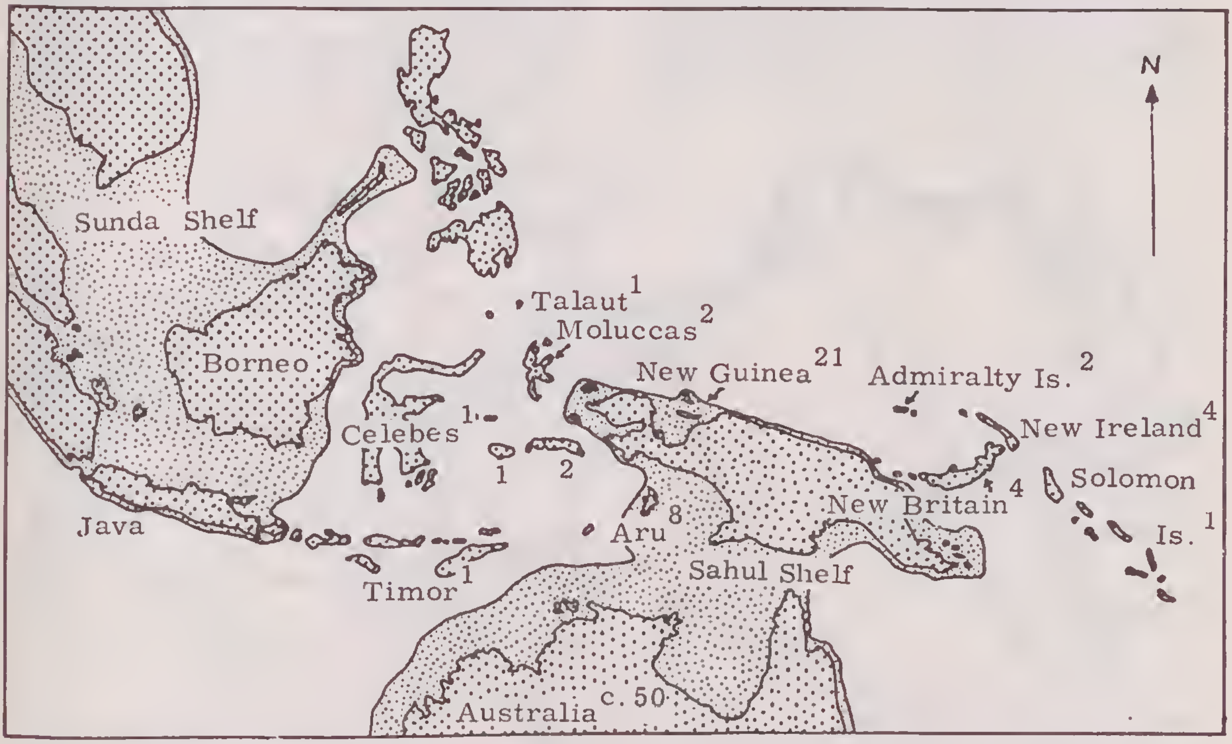

FIG. 4—Dispersal of marsupials. The traditional view is that a broken landbridge connects Asia and Australia. Marsupials crossed this ever discontinuous bridge from the former continent to the latter. The Continental Drift view is that Australia glided northwards carrying marsupials and they are now slowly dispersing across the broken landbridge to Asia. Based on Cox 1970. Numbers against names of areas indicate the number of marsupial genera there.

this field by enthusiastic "drifters" than in all other fields put together'. On this, Professor Hallam commented, 'Unfortunately it is hard to disagree with this statement'. The careful analysis by Professor Dorothy Hill (1970) of fossil coral reefs in relation to the drift of continents shows how easy it is to interpret too much into our evidence.

PLATE TECTONICS THEORY

Basic Ideas

The theory is always out of date. It is developing so fast that version follows version in rapid succession. For example, Gondwana has meant very different things at various times to various people, and ideas are still changing. However, the basic opinion remains the same—the rocks of the globe (lithosphere) are viewed as a series of relatively rigid plates, perhaps 20 in number (Fig. 5). Plate boundaries are of three kinds, viz. mid-ocean ridges, transform faults and ocean trenches. These are the zones along which the foci of earthquakes are concentrated.

Where plates collide, mountain ranges are pushed up. The high mountains of New Guinea are the leading edge of the northward drifting Australian plate. Australia is coming closer to Asia at a speed of probably 2-3 cm per year.

Transcurrent Faults Prove Mobility

Where the plates grind tangentially against one another, the vast transcurrent faults of the world are found (Wellman 1971, Fitch 1972). Examples are the Alpine Fault system of New Zealand and the San Andreas Fault system in North America. These fault systems are each hundreds of kilometres long, are of high energy, and may be associated with mountain building (having a vertical component also), with earthquakes and volcanic activity. They demonstrate a mobility in the earth's crust not suspected a century ago. The Alpine Fault system is associated with the Southern Alps of New Zealand, then runs up the west coast of the North Island (where Jurassic rocks are crushed, and earth movements are strong) and across the middle of that island where considerable thermal activity can be found.

The San Andreas Fault system is responsible for the rift that separates Baja California from the continental mainland, for the coastal mountain ranges, and for the notorious Los Angeles and San Francisco earthquakes. North of Los Angeles I have seen a fault zone a quarter of a

Fig. 5a—Australia, situated well away from the active tectonic plate borders, experiences mild tectonics. The double lines mark the mid-ocean ridges, where new material is added to the plate margins, while the single cross lines represent major transform faults. The thick lines are trenches where one lithospheric plate slides under another, often associated with ocean deeps. Arrows indicate the direction plates are moving with respect to one another. After Oliver, Sykes and Isaaks 1969.

kilometre wide, characterized by innumerable faults where strong rocks are mushed to meal.

The World as a Heat Engine

Then what is the enormous power that drives the rafts along? It is thought that far below the surface of the earth there is a series of vast convection cells that move slowly but surely to cause rifts and move rafts. The plastic rock is envisaged as moving slowly upward on each side of a rift, then outward, causing sea-floor spreading and the drifting of continents and ocean basins. This hypothesis has yet to be substantiated (see Wright 1966 on its application to the southwest Pacific).

Oceanographic Evidence

With the technological advance of some large nations and their consequent increased wealth, it has been possible to undertake continuous, very expensive but very revealing oceanographic surveys. Ways have been devised for mapping the ocean floors accurately, for making all kinds of measurements of their physical properties, and more recently for boring and sampling the floors of the deepest oceans, thousands of metres from the surface of the sea. The surveys proved the presence of mid-oceanic ridges (Fig. 5) centrally divided by rifts, and peppered with volcanoes and earthquake foci, while the geophysical measurements showed them to be high temperature zones oozing new rocks. Dating showed that the ages of the rocks increased overall away from the rifts. Palaeomagnetic measurements showed that there were corresponding bands of rock on each side of the rift. So emerged the idea of seafloor spreading—that the convection currents keep carrying away the rock from the rift, while new rock emerges to take its place.

If the seafloor is constantly spreading, where does all this rock go? It is believed to be subducted (withdrawn beneath the surface) at the edges of the continental plates where deep oceanic trenches exist and earthquake foci are concentrated. As a result of all these contrary pressures, it is hypothecated that the Atlantic Ocean is widening and the Pacific narrowing. Also there are dead ridges, where activity has ceased.

So according to the Plate Tectonics Theory, the earth's crust is very mobile on the scale of geologic time, though movement is difficult to measure on the scale of the human life span.

The Time of Drifting

Then when did all this mobility begin? When did Australia start moving? If the continents have drifted, were they once united? The theory is that in the Mesozoic a single land mass, Pangaea (Fig. 6) broke up, first separating Eurasia from

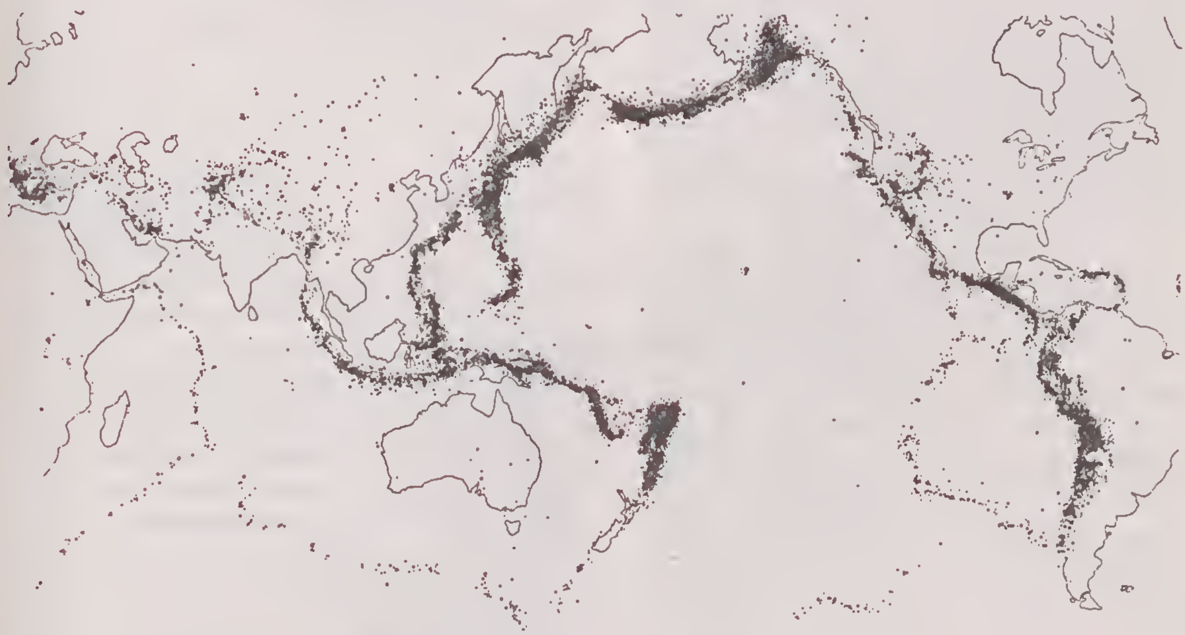

FIG. 5b—Dots represent the epicentres of earthquakes with focal depths greater than 100 km. After Barazangi and Dorman 1968. Their association with tectonic plate borders is very marked. Australia's position well within the Indo-Australian plate accounts for its relative freedom from such earthquakes.

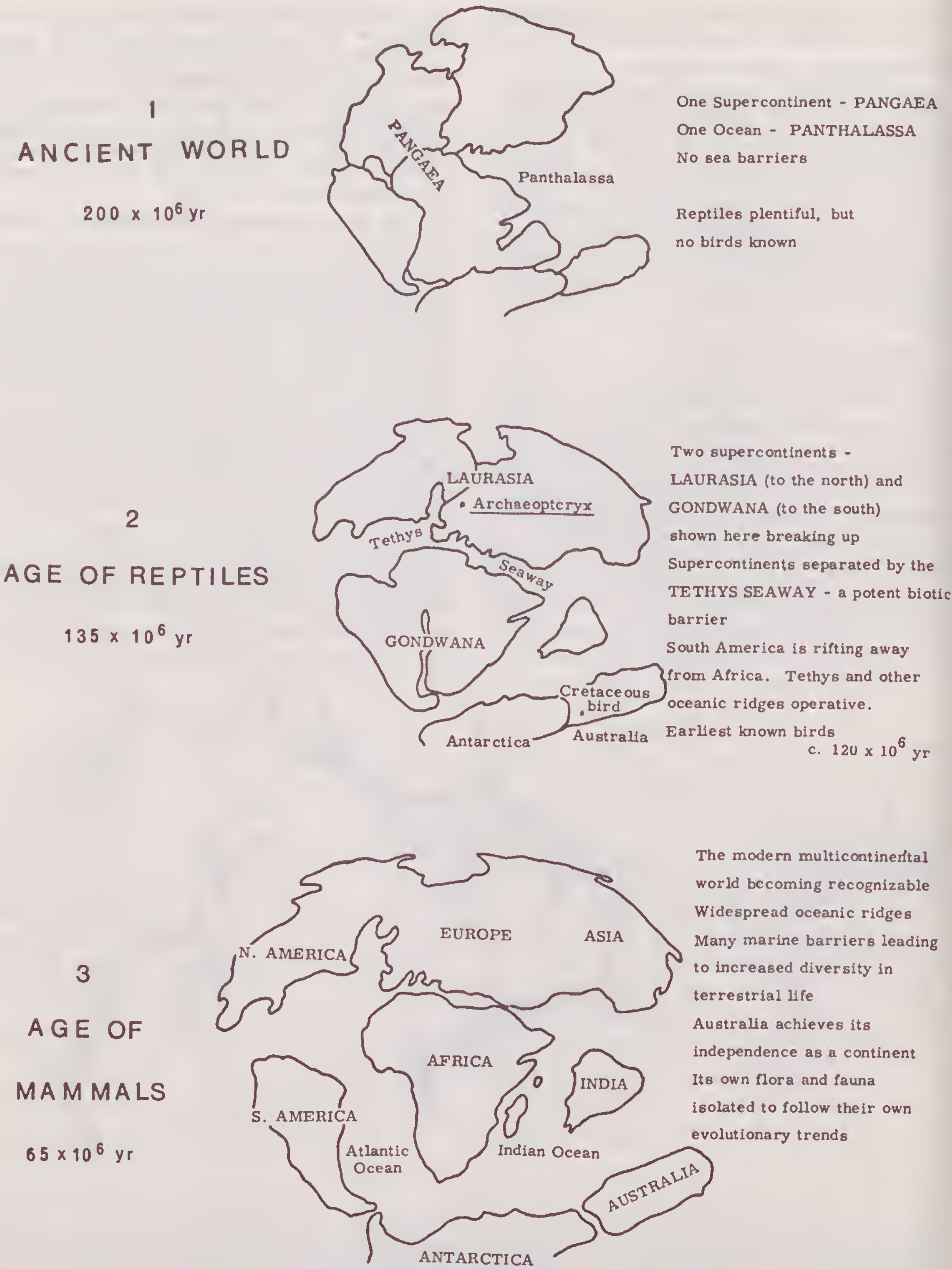

Fig. 6—Three stages in the evolution of the modern continents according to the Theory of Plate Tectonics. Australia's severance from other Gondwana countries and no subsequent contact with other land masses explains the unique elements in Australia's fauna and flora.

the block of southern continents, which split into South America/Africa and Antarctica/India/Australia. In the Upper Cretaceous to Eocene (between 100 and 50 m.y. ago) Australia is believed to have separated from Antarctica by rifting, and then later (probably much later) a mid-oceanic ridge developed that pushed Australia and Antarctica apart. Thus Australia began its northward drift.

Palaeomagnetism

The earth is a magnet, and its field is recorded in magnetically susceptible minerals. For example, as a lava flow from a volcano congeals, it freezes its magnetically susceptible minerals in the direction of the earth's field at the time. When the rocks containing these minerals are grossly changed in position by the drift of continents, the magnetic record appears to be chaotic. Palaeomagnetism sets out to discover the patterns of the earth's magnetic field in times past by re-orienting the rock masses of a given age. If the continents are moved so that the palaeolatitudes are in their correct positions, then they occupy places that fit also many geologic and biologic features.

THE EFFECT OF DRIFT ON AUSTRALIAN FLORA AND FAUNA

Looking at the world as a whole, it is difficult in the traditional view to explain the patterns of distribution of plants and animals, their great increase in diversity since the Mesozoic (Valentine & Moores 1970, Axelrod 1972), and the changing climates they indicate (Fig. 7). On the subject of diversity, for example, it may be noted that mammalian species have evolved during the Cainozoic in a relatively short space of time. Fifty per cent more orders of mammals than of reptiles have appeared in one third the length of time. Another feature is the contemporaneous development of similar forms in placentals and marsupials. Also even in the placentals, members of different orders perform the same functions in different areas. All this requires explanation, and the Plate Tectonics Theory has one to offer. A single continent (Pangaea) broke up during the Mesozoic. This in turn divided into the present continents, isolating their floras and faunas. The increase in the number of land masses meant an increase in the number of faunas and so greater diversification. Continent contacts permitted distribution. However, it must not be inferred that all the problems have been solved. In our present state of partial knowledge there are many unanswered questions (e.g. Meyerhoff 1970a, b, Meyerhoff & Teichert 1971).

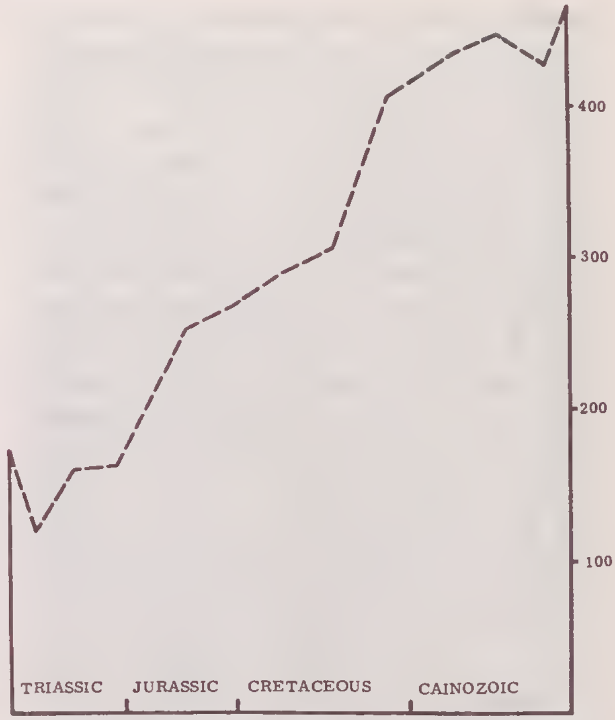

Fig. 7—Increase in biological diversity following continental drift. Increase in number of families during the Mesozoic and Cainozoic eras (After Valentine and Moores 1970).

One great event that must have profoundly affected the flora and fauna was the flooding of Australia by an epicontinental sea that turned it into a group of islands (Fig. 8), extending its coastline, changing its climates, and isolating biotas. At the same time great sedimentary basins were initiated, such as the Great Artesian Basin and the Murray Basin. It may be that the sinking of the land to admit the ocean was a result of the strain and stress set up prior to the break between Antarctica and Australia.

Another great marine event occurred in the Pleistocene Ice Age when a number of times the sea level fell very low as the great ice caps were built up, extracting water from the ocean. At those times New Guinea, the Australian mainland and Tasmania were one land mass, so that exchanges of flora and fauna could occur. However, the sea is not the only barrier. The Red Gum, *Eucalyptus camaldulensis* grows in every State of Australia except Tasmania. The reason appears to be that when the sea level was low enough for this tree to extend its range to Tasmania, the climate was too cold (Gill 1961a). A similar explanation has been given for the absence of mistletoe in Tasmania.

The break-up of a single land mass into a number of smaller areas increases the length of the coastline, and the extent of continental shelf available for the evolution and distribution of shallow water species, thus leading to a greater diversity. The climate also is changed through the loss or the lessening of continental effects, and the differences created between east and west coasts. The break-up of a land mass increases isolation of faunas, which leads to the emergence of new life forms. If at the present time Asia should break away from Europe, the coastlines of those continents would be lengthened, the continental climate of the Urals and Siberia would be considerably modified, new coasts would be established, new areas for shallow water marine organisms, and the flora and fauna of the region would be divided, thereafter tending to follow their own evolutionary lines.

In review, two ideas could not be more different than the static world (created ~ 6000 yr ago) of 19th century thought, and the modern dynamic concept of a pageant of life billions of years old on ancient continents drifting across the face of the earth and stimulating the evolution of new life forms.

THE LONGEVITY OF AUSTRALIAN FOSSIL GENERA

Echidna and *Ornithorhynchus* used to be regarded as relics from the Cretaceous age. Mr. Claude Austin of Western Victoria made a collection of bones from a cave at Strathdownie (Gill 1957a) which included the crania of *Zaglossus*, the New Guinea highland echidna, and beautifully preserved jaws of extinct kangaroos, and many other marsupials (Merrilees 1965). This finding stimulated the study of fossil monotremes, and it was discovered that:

Fig. 8—The Lower Cretaceous epicontinental sea of Australia. The division of the continent by this sea must have increased diversity, and is probably connected with the early radiation of Australian marsupials. The withdrawal of the sea made Australia one continent, and the present major drainage systems were established.

(a) Dun (1895) recorded *Proechidna* (= *Zaglossus*) and *ornithorhynchus* from auriferous beds near Gulgong, N.S.W., believed to be of Pliocene age, but all his material is *Zaglossus*. The site is a deep cave (*c.* 60 m) in limestone below basalt on which a deep red soil is developed. It was much easier to work out the stratigraphy while the gold mining was in operation than it is now. The Geological Survey concluded that the sediments with the fossils were younger than the limestone and older than the basalt. The auriferous deposits are part of a formation extending *c.* 24 m above the top of the caves they filled (Wilkinson 1877). The sediments also contained Tertiary fruits, reptiles, and other remains (Wilkinson 1887).
On the geomorphology, the soil on the basalt (cf. Gibbons & Gill 1964), the age of the basalt by analogy with those dated by marine fossils, and the stratigraphy revealed by the pits in diatomaceous earth at Home Rule, the original ascription of a Pliocene age is reasonable. However, Dalhunty (1971) has recently published a K/Ar age of 14·3 m.y. (average of two dates) for the basalt, i.e. Middle Miocene. On this evidence the Gulgong *Zaglossus* is the oldest monotreme so far found in Australia.

(b) On the Australian mainland and in Tasmania, *Zaglossus* was more common during the Pleistocene than *Echidna*, although the former is now extinct there. So instead of *Echidna* being a sole relic from the Cretaceous, it was dominated by *Zaglossus* as late as the Pleistocene, and probably in the Tertiary as well. *Zaglossus* is now limited to the highlands of New Guinea. It is a genus adapted to humid conditions, while *Echidna* is adapted to dry conditions. The record of *Zaglossus* from the Miocene is thus in keeping with the humid forest of that time. This facies was very widespread in Australia during the Tertiary, so it can be expected that suitable species had wide distributions. *Protemnodon otibandus* appears to be an example, as it has been recorded from New Guinea (Plane 1967), Queensland (Plane 1972), New South Wales (Marshall 1973) and Victoria (Plane 1972).

The development of Australian marsupial studies (e.g. Gill 1953, 1957b, Stirton 1957a, b, 1963, 1967, Woods 1958, 1960, Wakefield 1972, Ride 1964, 1970, Stirton, Woodburne & Plane 1967, Stirton, Tedford & Woodburne 1968, Tedford 1966, 1967a, b, Merrilees 1965, 1967, Woodburne 1967, Plane 1967, 1972, Plane & Gatehouse 1968, Turnbull & Lundelius 1970, Bartholomai 1967, 1970, Marshall 1973) shows an early establishment of the orders, and that many of the families are very old. On the other hand, many species are newly emerged (see below).

A NEW HYPOTHESIS

Finding the idea of Australia as a land of Cretaceous relics unacceptable, I prepared a six-page circular in 1962 setting out an alternative theory of the evolution of the flora and fauna. This was sent to some 200 correspondents round the world, and the response was very encouraging. It is asserted that *Australia is not a biologic asylum where ancient forms of life persist, but a continent with a life of its own. Rather than being ancient, much of the present flora and fauna are recent developments in response to climatic changes.* There has been failure to distinguish between the continuity of ancient patterns of organization (e.g. the monotremes) and absence of change.

AUSTRALIAN FLORAL EVOLUTION

Although the Australian flora is so distinctive, it contains ancient elements shared with other continents (e.g. Proteaceae) and derived from a common flora before the continents were separated. Where then does the Australian Cretaceous flora find its affinities? It has always been recognized that the correlatives existed in the other Gondwana countries—Africa, South America and India. The traditional view saw the Raj Mahal Cretaceous flora of India as an Asian flora shared with Australia, whereas the Plate Tectonics Theory sees India as a piece of Gondwanaland that (with the common flora) drifted north and collided with Asia, thus causing the crumpling up of the Himalayas.

Climatic changes have occurred. The traditional view is that these were world-wide, whereas the modern view says this is only one element, another being that the climate changed because of the northward drift of Australia during the Cainozoic. Certainly the evidence of the presence of ice in southeast Australia during the Lower Cretaceous cannot be explained on the traditional view, whereas it is what would be expected on the premises of the Plate Tectonics Theory (Gill 1972 and references).

It is difficult to imagine Australia without *Eucalyptus* and *Acacia*, but so it was. They are unknown in the Mesozoic, although angiosperms have been recorded from the Lower Cretaceous (Kenley 1954, Medwell 1954). Australia was then a cooler and more humid place than now.

On palaeomagnetic evidence, the South Pole was SE. of Tasmania (Wellman et al. 1969). The Plate Tectonics interpretation is that as Australia was rafted northwards 'into a zone of warmer drier climate, plant genera such as *Acacia, Eucalyptus, Casuarina, Melaleuca, Hakea* and *Eremophila* adapted to progressively drier, more continental climate (Fig. 9). And as drought continued to spread over the interior, new opportunities appeared for temperate austral families which evolved a wholly new flora composed of desert and desert-border alliances restricted to the drier parts of Australia' (Axelrod & Raven 1972). (See Fig. 10.) As will be seen later, the

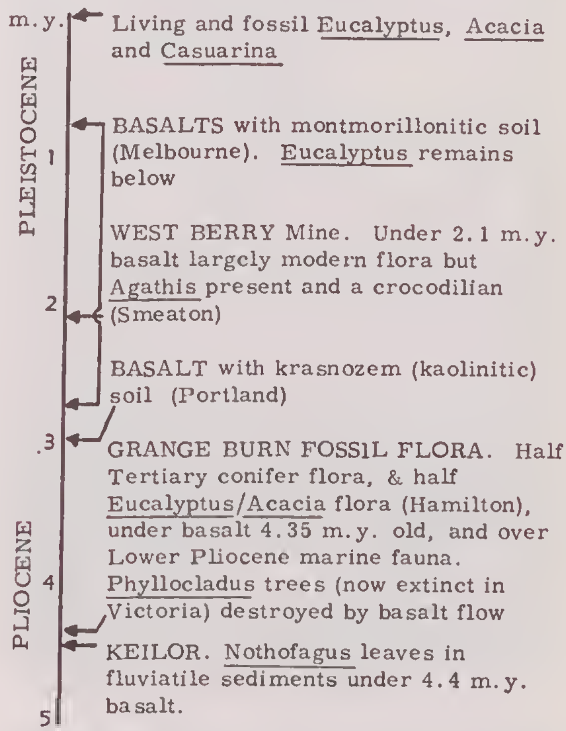

FIG. 9—Time-line showing dated southern Victorian sites that illustrate the transition in the Upper Cainozoic from the Tertiary conifer/*Nothofagus* flora (humid climate) to the present sclerophyll *Eucalyptus/Acacia* flora (comparatively dry climate). The Tertiary climate formed kaolinitic soils on basalts whereas the Quaternary climate formed montmorillonitic soils on them.

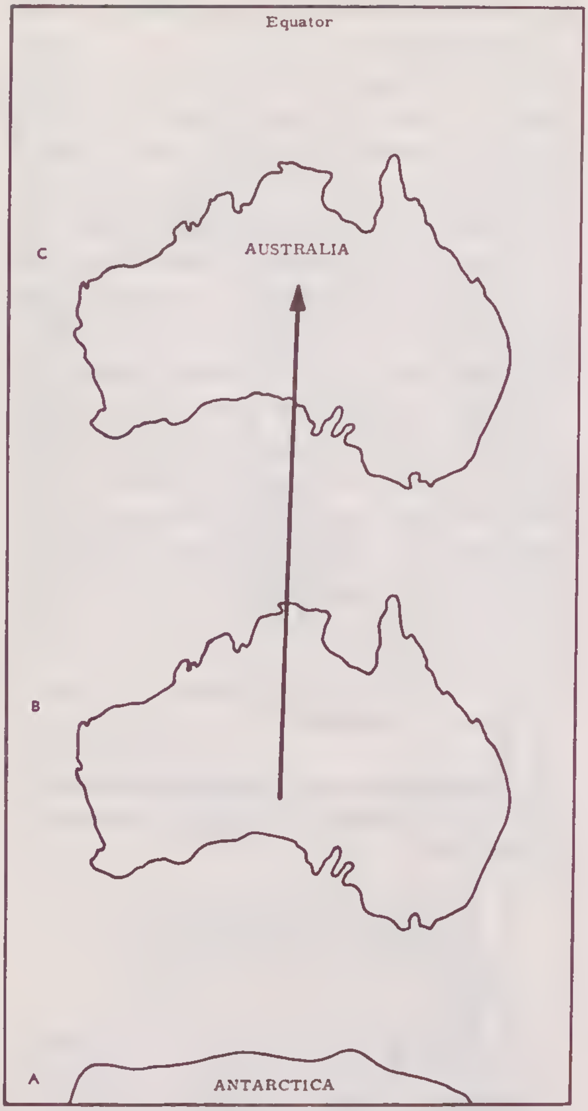

Fig. 10—The northward drift of Australia.
A. Australia's position in the Lower Tertiary in a cold and humid climate. B. In the Middle Tertiary the climate was humid and subtropical (in the south at least), due apparently to world climatic changes. C. The present position of Australia with a tropical climate in the north and two-thirds of the continent dry. These changes of latitude and climate through the Cainozoic brought strong pressure to bear on the flora and fauna.

palaeoclimatic picture is not quite as simple as that.

The earliest *Eucalyptus* wood is dated Oligocene (Gill et al. 1962); no pollen of *Eucalyptus* type (*Myrtaceidites eucalyptoides*) is known earlier than this. For a long time no *Acacia* earlier than the Pliocene could be found, but now 'the first appearance of *Acacia* pollen appears to occur at the base of the Middle Miocene in the Muddy Creek Marl (Harris 1971, p. 75).

If the world climate did not change during the Tertiary, and Australia drifted northward at a regular rate, then the climate would get gradually warmer and drier, as the present world desertic zone was reached. This is not what occurred. In the mid-Tertiary southern Australia had a tropical or subtropical climate. Large crocodiles existed as far south as Victoria. Kauri trees (*Agathis*) and *Araucaria* (which will not reproduce further south than Queensland now) grew in profusion as far as southern Tasmania. Laterite, the soil of the subtropical monsoons, was formed as far south as Tasmania. The contemporary marine faunas are such as are now found much further north.

Finally, the evidence of the oxygen isotope palaeotemperatures fits the biologic evidence (Dorman & Gill 1959, Gill 1972). The palaeoclimatic record for Australia in the Cainozoic is therefore at variance with what would be expected from a regular northward drift (Raven & Axelrod 1972). It is inconceivable that Australia drifted northwards into the tropics and then back again. The explanation is probably that the world climate altered, and that a wider tropic belt existed in the mid-Tertiary. There is much evidence round the world that this was actually so.

On present knowledge, three stages can be defined in the history of the Australian Cainozoic flora.

Stage 1

The Mesozoic fern/conifer flora was followed by a long period when rainforests were widespread in Australia. These existed in southern Queensland, New South Wales, Victoria, South Australia, and in Western Australia as far north as the Coolgardie district (Balme & Churchill 1959). How much further they extended has yet to be ascertained. The flora was rich in conifers (*Agathis, Araucaria, Podocarpus, Phyllocladus,* see Appendix 1), ferns and Southern Beech (*Nothofagus*). A typical deposit is the brown coal at Yallourn, Victoria, the fossils from which have been described by Cookson (1945, 1946), Cookson & Duigan (1950), Patton (1957), Duigan (1966) and others. Cookson (1945) showed that while no *Nothofagus* wood had been discovered in the coal, the pollen of this genus was very abundant (c.f. Duigan 1966), sometimes enough to form pollen coal. The conclusion was that while the conifers and other trees grew on the swamp flats, *Nothofagus* occupied the well-drained slopes, as it does today.

STAGE 2

This covers a period of two or three million years during which a slow changeover occurred from the humid rainforest conditions to the present aridity. On Grange Burn in Western Victoria (Gill 1957b) there is a geologic section with carbonaceous deposits between Lower Pliocene (Kalimnan) marine beds and a basalt dated 4·35 x 10^6 yr by K/Ar. The carbonaceous deposits reveal a flora more or less half and half of the Tertiary rainforest (conifer/*Nothofagus*) and the present (*Eucalyptus/Acacia*) flora. In the Smeaton district of Victoria, basalt from a bore at the West Berry Consols mine, about 2 km west of that town, is dated 2·11 m.y. by K/Ar (Aziz-ur-Rahman & McDougall 1972). Beneath it a clay has a pollen assemblage indicating a flora like the present, but not far away *Agathis* was found, and the bones of a crocodilian genus, showing that the change to the present climate was not yet complete.

On the Murray River, a bed considered to be at or near the base of the Pleistocene (taken at ca. 1·8 x 10^6 yr) yielded a palynologic profile like the present one (Churchill 1973, Gill 1973a). This change from rainforest to sclerophyll flora for a large part of Australia is a major and far-reaching event. It provided a wide range of new opportunities for sclerophyll genera. *Eucalyptus*, *Acacia* and other genera extended to form the widespread savannah woodlands and sclerophyll forests we now know. These in turn have strongly affected the animal life, especially the tree-dwellers and ground-living forms. Furthermore, the wide extension of desert and desert-border ecologies has brought about the proliferation of species fitted to these habitats. *Acacia*, first known in the Middle Miocene, has now some 400 species, and it is considered that this radiation is to a large extent a function of this climatic change from humid to dry conditions.

The genera of Eucalyptus and Acacia are remarkable for their diversity, and notorious for the problems presented in their taxonomy. Of living forms alone, some 600 species of *Eucalyptus* have been described, and some 400 endemic species of *Acacia*. *Many Eucalyptus species are very difficult to define because of great variation and much hybridization. The intense speciation and the taxonomic instability suggest a process of radiation.* The process of differentiation began in the Upper Miocene or Pliocene, and came into full force in the Pleistocene when the *Nothofagus* and conifer forests became reduced in extent and in number of species, and restricted to comparatively small areas of high rainfall. Thus the full opportunity for the above two genera to expand came only about two million years ago. During the past 2 m.y. there have been considerable oscillations in both temperature and humidity in Australia associated with the glacial/interglacial cycles. The changing climate would mean selection, and multiplication of opportunities for new adaptations. In eastern Australia the period was also one of tectonic change. The quick-changing climatic oscillations of the Quaternary are still taking place, and it is interpreted that *Eucalyptus* and *Acacia* are still in process of radiation and adaptation. The very variable environment has led, it is thought, to their extensive variation and many unstable species. *Eucalyptus* and *Acacia* apparently suited the Quaternary conditions, and were flexible enough to succeed in spite of the many and great changes in Quaternary climate. *What has been said about the two foregoing dominant tree forms, no doubt applies to many other plants.*

STAGE 3

This is the present floral stage, characterized by widespread desertic and sclerophyll types of vegetation. As Australia is the driest continent, it is pertinent to enquire when these desertic conditions began and how they spread. On the north bank of the Murray River a short distance east of the South Australian border, a deposit of probably lowest Pleistocene age includes pollens and spores indicating a flora the same as the present semi-arid one (Churchill 1973, Gill 1973a), but below it is a laterite, indicating subtropical monsoonal rainforest conditions. This marks the time of incoming of the present aridity in SE. Australia. Some zoologists claim that the taxa which are the object of their studies indicate a long period of evolution in desertic conditions. Geological evidence as at present available suggests that the northwest of Australia has been dry throughout the Cainozoic, so one envisages the evolution of desertic forms there, later to spread and radiate when the rainforests retreated.

So two radiations appear to have occurred in the flora:

(a) when the Australian rainforest floras developed in the Lower Tertiary, and

(b) when the rainforests departed and the present dry regime became established.

Many genera have become extinct or very restricted in distribution on the mainland of Australia, but others appear to have adapted themselves to the new conditions. An example is *Microcachrys* which presently occurs only on the high plateau of Western Tasmania. It grows in that cold, wet environment as a recumbent shrub in a hostile ecology, but in the Cretaceous it was a widespread forest tree. When I went to the National Museum as palaeontologist in 1948, I noted some beautifully preserved silicified coniferous wood with an inadequate locality specification, and decided as opportunity was offered to find out where it came from. Other pieces came to light, but not the locality, until many years later a schoolteacher brought in a large piece, providing at the same time an approximate locality. The farmer on whose property it occurred near Casterton showed me the remains of a large log of this wood, from which he said people had been taking pieces for many years. Mr. H. D. Ingle of CSIRO Wood Structure Section kindly examined the wood and determined it as *Microcachrys*. A photograph and description of this wood by him appears as Appendix 1 to this paper.

In the meantime Cookson (1947) recognized pollen of this genus and described it as *Microcachrydites antarcticus*. Dettmann (1963) later documented its distribution and referred to its dominance (p. 122). Harris (1971) reported it as late as the Oligocene on the mainland (p. 74).

So the abundant forest tree of the Cretaceous has become a relict recumbent shrub of a difficult and limited environment.

EVOLUTION OF THE AUSTRALIAN FAUNA

The Environment

The Australian continent we know came into existence in the Upper Cretaceous, when the Lower Cretaceous epicontinental seas (Fig. 8) that had turned it into a group of islands finally withdrew. This was a most important event, widespread in its consequences. As Tappan and Loeblich (1972) point out, 'Advancing or retreating epicontinental and shelf seas, and changes in continental position and height, affected atmospheric and oceanic circulation and climatic regime, causing variations in nutrient supply and fluctuations in productivity and food resources'. With these dramatic geologic, geomorphologic and climatic changes came the angiosperm revolution (Gill 1961b), the demise of the Age of Reptiles and the ushering in of the Age of Mammals. Such fossils as are known show that there was an early radiation of the marsupials, and this in time (and also no doubt in aetiology) was connected with the physical changes. When Australia achieved its continental unity by the withdrawal of the invading seas, the great river systems such as the Murray/Darling were instituted. However, the greater humidity of the Tertiary meant much larger rivers than now. The copious acidic waters deeply leached the country rock, so establishing the Nunawading Terrain (Gill 1964) with its kaolinites and bauxites which are now the basis of many industries. Then as the tropical belt retreated northwards, a belt of monsoonal climate crossed the continent, forming the Timboon Terrain with its widespread laterites, also now the basis of many an industry. Tertiary laterite and other deeply leached profiles cover some $1{\cdot}5 \times 10^6$ km^2, a feature which makes Australia different from every other continent. Australia is a continent of small tectonic movements. The Plate Tectonics Theory provides an explanation of this; it is in the middle of a large plate. Mountain range systems are formed at the edges of plates, where they collide with others. Australia's surface has been little disturbed and ancient soils such as the bauxites and laterites are widely preserved. On the Great Dividing Range erosion did occur, and the deeply leached rocks were washed away leaving rich deposits of gold from Palaeozoic rocks. This is why Australia had gold rushes in its early history.

On the other hand, Australia's flora and fauna had to evolve so as to be able to cope with these impoverished deeply leached soils. The first settlers came from Europe where the Pleistocene ice sheets like giant bulldozers had cleared away old soils; young soils developed on this new surface and on the loess of periglacial areas. So the early settlers were puzzled by the ancient soils they found here. CSIRO invited an international soil expert to visit Australia and he began by spending two months in South Australia where he saw laterites, red earths and such. When he came to Victoria and saw the young soil (chernozem) on the Keilor Terrace of the Maribyrnong River, he said it was the first soil of a type he knew that he had seen since landing in Australia.

With the change from the humid Tertiary climate to the modern rather arid one, the flora and fauna had to cope not only with poor soils but also with lack of water.

Effect of Open-Crown Forests on Fauna

New forests mean new animals; they migrate or evolve, or both. When the rainforests departed and the open sclerophyll forests became established, a powerful pressure for change was exercised on the fauna. This did not happen rapidly, but took a couple of million years, so the fauna had time to adapt and evolve. The biologic and geologic changes are greater than would be achieved simply by a northward continental drift $\sim$ 500 km (2 m.y. at $2{\cdot}5$ cm/yr), which means that apparently a factor of world climatic change is also involved. Other evidence is believed to favour such a change.

The new forests had open crowns instead of closed ones. Volant mammals have limited opportunity in the thick crowns of rainforest trees, but they can proliferate in the open cupolas of the sclerophyll forests.

Leadbeater's Possum (*Gymnobelideus*) was long thought to be extinct, but was then rediscovered (Wilkinson 1961). It is a non-volant form remarkably like the volant *Petaurus*. *Petaurus* evolved from *Gymnobelideus*, and skeletally they are so much alike that this must have been a recent event. Indeed it was not until detailed work was done that the skeletons of the two genera could be distinguished. They were made different genera on the presence or absence of the flying membrane.

Further detailed work by the late N. A. Wakefield (not previously published but made available by him to me) has shown that the divergence of one genus from the other is a Quaternary event. Pleistocene *Gymnobelideus* has the same limb proportions as the living form (cf. Wakefield 1960), but in *Petaurus* there is a major elongation of the radius and ulna compared with other limb bones. Wakefield was able to trace this change against time. Radiocarbon dates prove that the *Petaurus* of 15-17,000 years ago in Victoria were less slender and less elongated in the limbs than are the living *Petaurus*. That length of time ago, the forelimb bones of *Petaurus* were about midway between *Gymnobelideus* and modern *Petaurus* in the proportion of bone length to width —an adaptation to the flying habit (Fig. 11).

It cannot be inferred that twice as long ago the *Petaurus* flight limb bones had the same proportions as *Gymnobelideus*, or (a different thing) that it became volant at that time. By analogy, one would expect more time to be involved. However, it can be said that much of the adaptation of the flight limb bones of *Petaurus* has taken place in the past 20,000 years, i.e. evolution is in process from the non-volant to the volant.

The gliding membrane of *Petaurus* is well developed, as it extends right to the manus and not just to the elbow; also there is extra hair on the 5th digit compared with *Gymnobelideus*. Its flight is effective and rates at about 9 m per second. The flight path makes an angle of the order of 30° with the ground. *Petaurus* can bank and swoop. Unlike *Schoinbates* it glides when spotlighted. One interesting adaptation of *Petaurus* as a glider is that it has a wider habitat tolerance than *Gymnobelideus*.

The plexus of *Petaurus* species, subspecies and varieties has not yet settled into a group of well defined species, so differences of opinion on

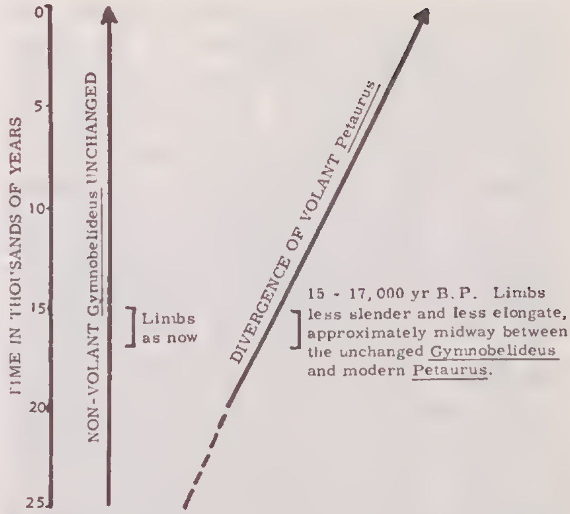

FIG. 11—Radiocarbon dates show that in the past 20,000 yr the volant *Petaurus* has been diverging from the very similar but non-volant *Gymnobelideus* which has remained unchanged (information from the late Mr. N. Wakefield). This is interpreted as part of a contemporary radiation of mammals to fit the modern *Eucalyptus/Acacia* flora.

classification such as have occurred are not surprising. The group is still in radiation.

Just as *Petaurus* is a volant form closely related to *Gymnobelideus*, so *Schoinbates* is a volant form closely related to the non-volant Ringtail Possum *Pseudocheirus*. These represent a second line of evolution of volant forms from non-volant. The former has the femur, tibia and fibula significantly elongated relative to the latter, Wakefield points out, but the humerus less so. The radius and ulna are proportionately much less elongated. *Schoinbates* has a flight path of the order of 40°, and avoids windy conditions, which *Petaurus* does not. *Schoinbates* is sedentary in habit relative to the migratory habits of *Petaurus*. *Schoinbates* feeds on eucalypts, while the non-volant *Pseudocheirus* takes a variety of plants for food.

Acrobates represents a third evolutionary line of flying possums, and is related to the pigmy possums. It may be the most primitive. A subspecies in Queensland appears to be a recent development. Thus there has been in geologically recent time a wide adaptation of flying forms to take advantage of the new ecologic feature—the open crowns of the eucalypt forests.

Effect of Open Forest Floors

The new forests had open floors as well as open crowns. They had light, even direct sunlight, on the floor. The floors were also warmer and drier than those of the rainforests. They were a new factor of profound ecologic importance.

Large mammals do not normally inhabit rainforests because of restriction to movement, but they do inhabit open forests. Large ratite birds typically belong to the open forests and plains. The new forests allowed the entry of kangaroos and wallabies, and a host of smaller animals. Opportunity was provided for phascogales (brush-tailed marsupial rats) to expand in species and numbers. Placental rats changed their distribution. The increased areas of open country provided new opportunities for bandicoots, in which also there seems to have been a radiation.

Emergence of the Grasses and Kangaroos

Much remains to be done to clarify the history of grasses in Australia. In the rest of the world the emergence of grasslands as a major habitat led to the evolution of the large grazers such as the horse and cow. The ecologic equivalent in Australia is the kangaroo and the proliferation of macropodid species in the late Cainozoic may be associated with the emergence of extensive grasslands. It is likely that in the mid-Tertiary there were grasslands and savannah woodlands in areas now desert, in which the macropodids described by Stirton and others were present. However, Gramineae pollen certainly becomes abundant in the Pliocene and this is an ecologic fact of great importance. It seems that extension of grasslands provided an opportunity for the kangaroos and related animals to radiate, giving the very rich Quaternary faunas, later impoverished.

Effect of Extension of Grasslands and Deserts

With the retreat of the Tertiary rainforests, their areas were replaced with sclerophyll forests, savannah woodlands, grasslands and deserts. With this change in ecology, there had to be changes in fauna. Numerous Australian animals are adapted to desert and desert margin conditons. The close relationships of some species-groups suggests comparatively recent evolution. For example, the rat kangaroos (four genera) are notably difficult to separate as species and appear to represent a recent radiation. They are characteristic of grassy country, rocky outcrops and bush country. *Caloprymnus* is specialized for the desert. As with many other groups, there are Tasmanian variants of the mainland species.

Evolution of Australian Birds

Penguins, ratites (ostrich, emu, cassowary, moa, rhea and such) and some other birds are limited to the Southern Hemisphere, a fact that requires explanation. The Plate Tectonics Theory postulates that these birds evolved on Gondwana after it separated from Laurasia. The earliest known birds are:

(a) *Archaeopteryx* from the Solenhofen Limestone of late Jurassic age in Germany—a Laurasia bird.

(b) *Unnamed bird* known by feathers only from Lower Cretaceous in Victoria—a Gondwana bird.

These birds are not very different in age, and the detail of development in each suggests considerable evolution from reptile stock before their appearance. It is not known where the first fossil birds evolved. It could be Australia, or Europe, or somewhere else. An interesting possibility is that birds are descended from two stocks (Laurasian and Gondwanan). However, when flapping flight evolved, birds could fly from continent to continent. Thus the majority of present Australian birds are related to Asian families (Cracraft 1972).

Penguins, as Gondwana birds, are of special interest to our subject. They are known from the Eocene and Oligocene (Glaessner 1955, Simpson 1957), and the Miocene (Simpson 1959, 1966, 1970) of Australia.

Ratites are of interest because they also are Gondwana birds. Little is known yet of their early history, but the avifauna in the past was richer than now, when the emu and cassowary are the only ratites in Australia. Stirling and Zietz described the huge extinct *Genyornis* (Stirling 1900, Stirling & Zietz 1896a, b) from the bed of the dry Lake Callabonna (Stirling 1900b) in Central Australia. I found the footprints of a bird of similar size (central toe over 20 cm long) in the Last Interglacial aeolianite at Thunder Point, Warrnambool. Other footprints in the same formation show that other birds were also present. Bell and De Merlo (1969) recorded a ratite from aeolianite that I consider to be also Last Interglacial in age at Venus Bay, Gippsland. At the request of Mr. and Mrs. Lyndon I examined the site, and think that the tracks are of two birds, one walking behind the other. The footprints are similar in size to those of an emu, but have a pronounced hallux print which is not present in emu spoor. Thus as recently as the Last Interglacial (about 125,000 years ago) there were at least two ratite birds which are not present now.

The Recent Faunal Impoverishment

During the Upper Pleistocene, adversity overtook the Australian fauna as it did in many parts of the world. In addition to the birds, numerous species of kangaroos, wallabies, wombats and other groups of marsupials died out. The largest marsupial that ever lived, *Diprotodon optatum*, failed to survive, as did all its family. Also, the whole family represented by the curious marsupial *Thylacoleo carnifex* came to an end. The fact of the impoverishment of the fauna is well established, but the reason is not clear. Merrilees (1968) believes that man is the destroyer, but many of the extinctions occurred before man arrived in Australia (on present knowledge of his arrival date or likely time of coming). Even with all the scientific know-how and the technologies now available, we cannot wipe out a virile species like the rabbit, and it is unlikely that Aboriginal man could destroy a virile species. That is, Aboriginal man could hasten the demise of a species already failing, but he could hardly be the cause of extinction. In Africa, where man has been longest of all (Fig. 3), many giant forms still survive.

The impoverishment of the fauna left gaps which other species could fill, and niches which could bring about the evolution of new forms. Active evolution must be going on now to adjust to the faunal debacle, but the scale of time is such that we cannot see any significant change in a lifetime.

Some writers have blamed the dingo for causing the faunal impoverishment. However, many extinctions took place before the first Aboriginals arrived, and the dingo came with a later migration. Moreover, the dingo cannot expunge the rabbit either.

Now there is a new factor—European man and his massive machines. Earlier this century, an Australia-wide effort was made to wipe out the emu, and large amounts of money were spent on the scheme (Marshall 1966, p. 61). In spite of the slaughter, the emu continued. What the shooters, poisoners and egg-smashers could not do, land-clearers do without trying. The emu will breed only in the bush, so where the land is completely cleared, the emus have ceased to exist.

In addition to the faunal impoverishment in the late Quaternary, there have been some remarkable changes in distribution. The Tasmanian Tiger, *Thylacinus*, once present over the whole of Australia is now doubtfully surviving in Western Tasmania. The Tasmanian Devil, *Sarcophilus*, was also once to be found all over Australia, but is now limited to Tasmania. This genus suffered a retreat to the south. By contrast, the anteater *Zaglossus*, once present over the whole of Australia, has retreated north to New Guinea (Fig. 12). We do not yet understand these patterns of species retreat (limitations of distribution).

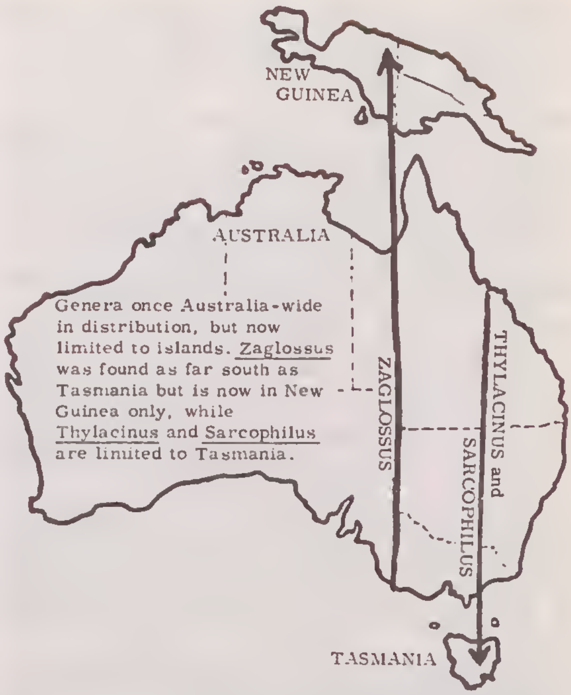

FIG. 12—As part of the Late Quaternary faunal impoverishment, these genera limited their distribution from the whole of Australia to bordering islands. Some retreated to the north and some to the south.

CONCLUSION

The unique character of the Australian fauna and flora is now well defined. The Theory of Plate Tectonics offers an acceptable explanation of more factors than the traditional view, but there is still a great deal that is not understood.

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